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Research Article

High temperatures and drought affect the germination of *Populus luziarum* and *P. primaveralepensis*, endangered species from the Neotropical region of Mexico

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Abstract

The higher temperatures and lower rainfall generated by global warming can have negative repercussions on the physiological responses of plants. This study aims to understand how the higher temperatures and declining precipitation will affect the germination of *Populus luziarum* and *P. primaveralepensis*, two endangered endemic species from western Mexico. The germination of these species was evaluated through the combined effect of three temperatures (24, 28, and 32 °C) and five water potentials (0, −0.07, −0.15, −0.3, and −0.6 MPa). The evaluated response variables utilized were the minimum time that seeds need to begin germination, the mean germination rate, and the final percentage of germination. Significant differences were found in the germination of both species due to the factors and their interaction. The highest germination percentages were registered with the combination of 24 °C and 0 MPa for both species (90% and 94%, respectively). The lowest percentage for *P. luziarum* was recorded at −0.6 MPa for any temperature (26–32%), while the lowest germination (23%) was found for *P. primaveralepensis* at −0.6 MPa and 32 °C. In addition, germinability was slowest in both species because of the highest temperatures and lowest water potential and their interactions. It is concluded that higher temperatures and drought stress will negatively affect the germination and recovery of populations of these two species.

Key words: Global warming, riparian forest, very fast germination, water potential

Introduction

The genus *Populus* L. (Salicaceae Mirb.) is comprised of 32 species of cottonwoods, primarily distributed in the temperate regions of the Northern Hemisphere (Kim 2018). Mexico hosts 11 species, four of which are endemic to the Neotropical Region. Among these, *Populus luziarum* and *P. primaveralepensis* are species that have fewer than 250 mature individuals and occupy a restricted area of less than 100 km^2. These characteristics suggest that they may qualify as endangered under the IUCN Red List criteria due to their small population sizes and limited distribution (Vázquez-García et al. 2017, 2019; IUCN 2022).

Cottonwoods are predominantly distributed in wetter regions, such as eastern North America, while in western North America and some areas of Mexico, they are confined to riparian habitats (Rood et al. 2003). Riparian ecosystems in regions with seasonal climates or arid conditions are characterized by significant fluctuations in water availability and temperature, often resulting in water stress (drought) during winter and spring (Drezner and Fall 2002). In response to water stress, adult poplar trees exhibit physiological and morphological changes, including reduced stem growth, smaller leaf size, premature leaf senescence, branch dieback, and increased mortality rates (Rood et al. 2003; Rosso et al. 2023).

In these habitats, cottonwoods face severe challenges due to water scarcity and increased temperatures as the topsoil dries following the lowering of the water table (Van Splunder et al. 1995) during seed germination and seedling establishment, two critical stages for plant recruitment (Harper 1977; Huang et al. 2016). However, very fast germination in *Populus* species serves as a key adaptive strategy, enabling these plants to exploit short windows of favorable moisture before conditions become hostile. This ensures seedling survival and supports population maintenance in environments shaped by extreme and unpredictable fluctuations (Karrenberg et al. 2002; Fall et al. 2007; Parsons 2012; Parsons et al. 2014).

Populus seeds are small, with reduced storage tissue and a thin coat filled with cotyledons (Drezner and Fall 2002; Karrenberg et al. 2002; Fall et al. 2007). *P. luziarum* and *P. primaveralepensis* seeds share these characteristics, measuring between 0.2 × 0.1 mm and 0.3–0.7 × 0.2–0.4 mm in length and width, respectively (Jacobo-Pereira et al. 2022). They are dispersed in riparian environments mainly by water and wind. Some seeds are deposited far from streams, where they experience extreme environmental changes because of their sensitivity to desiccation. These poplar seeds, classified as recalcitrant (Gosling 2007), exhibit low dehydration tolerance, high water content at maturity, and elevated metabolic activity at dispersal. As a result, they are highly sensitive to desiccation, can only germinate in the current season, and do not form a persistent seed bank (Müller-Starck 1982; Lefebvre et al. 2022). Germination of *P. luziarum* and *P. primaveralepensis* decreases after two weeks of storage under ambient conditions (Jacobo-Pereira et al. 2022).

Studies on Salicaceae have demonstrated very fast germination, with the highest germination percentages achieved in less than 24 hours within a temperature range of 15 °C to 35 °C. However, drought stress drastically reduces germination percentage or germinability (Farmer and Bonner 1967; Siegel and Brock 1990; Douglas 1995; Braatne et al. 1992; Li et al. 2006; Parsons 2012). Therefore, moisture and temperature are critical determinants for species germination and distribution in riparian communities (Siegel and Brock 1990; Schütz et al. 2002; Li et al. 2006).

Despite these insights, the combined effects of high temperatures and drought stress on germination in *Populus* species in temperate climates have not been studied. This knowledge gap is particularly important given climate change predictions for western Mexico, which estimate temperature increases of 2 °C to 4 °C and precipitation decreases of 10% (Ibarra-Montoya et al. 2011; IPCC 2014; Ruiz-Corral et al. 2016). Such climatic changes could significantly reduce the germination success of *P. luziarum* and *P. primaveralepensis*.

Methods

The *Populus luziarum* population is located along La Virgen stream (20°48'53.22"N, 103°34'51.30"W, at 1445 m a.s.l.), where the annual average temperature is 20.6 °C and annual precipitation is 909 mm. Meanwhile, the *P. primaveralepensis* population occurs along La Lobera stream (20°18'00"N, 103°35'59.9"W, at 1470 m a.s.l.) within the Bosque La Primavera Flora and Fauna Protected Area, which has an annual average temperature of 20.6 °C and annual precipitation of 983.6 mm (Fig. 1) (Ruiz-Corral et al. 2018; CONAGUA 2022; Jacobo-Pereira et al. 2022). Both species are found in riparian forests within the western portion of the Trans-Mexican Volcanic Belt, specifically in the Neotropical Region.

In October 2021, approximately 250 catkins with mature capsules were collected from at least 10 trees of each species. The catkins were placed in Ziploc bags and transported to the Center for Studies in Ecological Interactions of the Universidad de Guadalajara. The bags were manually shaken, and 3,000 seeds were extracted for each species. These were placed in sterile glass bottles, sealed, and stored in a refrigerator (TOR-REY, model R-14) at 4 °C to avoid seed viability loss (Jacobo-Pereira et al. 2022). Seed germination was evaluated at three temperatures and five water potentials.

The temperature levels were selected based on their ecological relevance: 24 °C was identified as optimal for both species, yielding the highest average germination percentages in freshly collected seeds and after storage treatments (Jacobo-Pereira et al. 2022). The 28 °C level corresponds to the maximum average temperature recorded during the seed dispersal period in their natural habitat (CONAGUA 2022), while 32 °C represents the highest temperature naturally encountered by mature seeds of both species and aligns with a projected temperature increase of > 4 °C under the A2 climate change scenario and RCP4.5 (Ruiz-Corral et al. 2016, 2018). The selected water potential levels reflect values reported for various soil types globally and have been previously tested on riparian forest species (Cooper et al. 2003; Li et al. 2006; Dürr et al. 2015). To simulate soil moisture variations, four polyethylene glycol (PEG 8,000) solutions at different concentrations were prepared with distilled water and stirred for 16 hours at 20 °C, following Michel (1983). For the 0 MPa treatment, only distilled water was used.

A total of 1,500 seeds were tested under the corresponding treatments for each species: five replicates of 20 randomly selected seeds per treatment. Seeds were placed in sterile plastic Petri dishes (60 × 15 mm) lined with cotton as a substrate and moistened with 5 ml of the respective water potential solution at five levels (0, −0.07, −0.15, −0.3, and −0.6 MPa). Lower values of water potential simulate increased water stress, representing drought conditions (Michel 1983). Each dish was sealed to prevent evaporation. The Petri dishes were distributed among three germination chambers (LUZEREN, model SPX250) with a 12-hour photoperiod, set to fixed temperatures of 24, 28, and 32 °C.

Germination was recorded when the radicle emerged (Baskin and Baskin 2014) and was evaluated hourly over 48 hours, as *Populus* species exhibit very fast germination, often reaching their maximum percentage within the first 12 hours (Siegel and Brock 1990; Karrenberg et al. 2002; Parsons 2012).

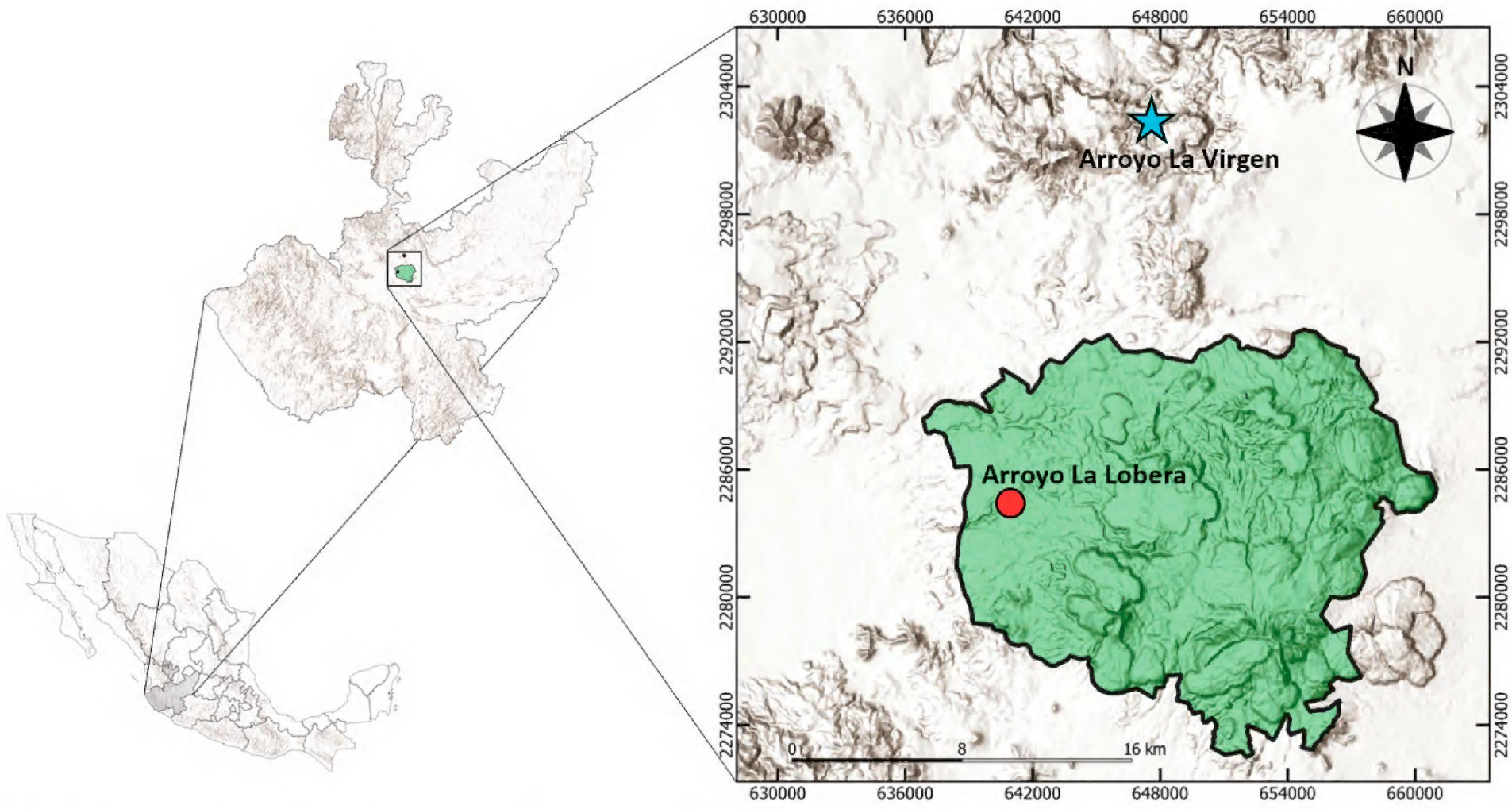

Figure 1. Study and seed collection sites in Jalisco, Mexico. Blue star: *Populus luziarum*, La Virgen stream; red circle: *Populus primaveralepensis*, La Lobera stream; green polygon: Bosque La Primavera Flora and Fauna Protected Area.

Although no germination was observed after 24 hours, the evaluation period was extended to 48 hours to account for any delayed responses. The response variables analyzed were (a) germination percentage at the end of the experiment (24 hours), (b) the time required for seeds to initiate germination (T_{min}), and (c) the mean germination rate in hours (MGR). MGR is the reciprocal of the mean germination time, which is the average time to germination and was used as a speed index (Soltani et al. 2015). It was calculated according to Ranal et al. (2009), using the following formula:

$$\mathrm{MGR} = 1/\left(\frac{\sum_{i=1}^{k} n_i t_i}{\sum_{i=1}^{k} n_i}\right)$$

Where n_i is the number of germinated seeds in the i^{th} time, k is the last hour of evaluation, and t_i is the time from the beginning of the experiment until the i^{th} observation given in the corresponding experimental unit.

To obtain the final germination data, the GerminaR library was used. Final germination percentages and MGR were analyzed using a Shapiro–Wilk test for normality and a Bartlett test for homogeneity of variances (Crawley 2012). A two-way analysis of variance (ANOVA) was conducted to evaluate the effects of temperature (three levels), water potential (five levels), and their interaction on germination percentages and MGR. A Student–Newman–Keuls multiple comparison test ($\alpha = 0.05$) was used to examine differences between treatments in all analyses. A Kruskal–Wallis test was applied to the T_{min} data of both species because the assumptions for parametric tests were not met, even after transformation. Significant differences between groups were evaluated using multiple comparisons with the Holm procedure ($\alpha = 0.05$). All statistical analyses and graphics were performed using R v. 3.5.2 (R Core Team 2018).

Results

The germination percentage of *Populus luziarum* was affected by temperature ($F = 26.42$, $p = 0.001$), water potential ($F = 78.43$, $p = 0.01$), and the interaction of temperature × water potential ($F = 3.95$, $p = 0.001$) (Fig. 2a). In general, there was a trend of decreasing germinability with increasing temperature and water stress, but this pattern was not observed for some treatment combinations. In the 0 MPa treatment, germinability decreased with increasing temperature. However, this trend at −0.07, −0.15, and −0.3 MPa was observed only at 32 °C, as there were no statistical differences between 24 °C and 28 °C. In contrast, in the −0.6 MPa treatment, germinability was significantly lower than in all other water potential treatments regardless of temperature, with an average germination of 29%. At 24 °C, the germinability of the control treatment (0 MPa) was significantly higher than in all other water potential treatments, but at 28 °C and 32 °C, there were no differences among the other treatments, except for the −0.6 MPa treatment, in which germinability was the lowest.

The germinability of *Populus primaveralepensis* decreased significantly with increasing temperature ($F = 46.34$, $p = 0.001$) and decreasing water potential ($F = 98.97$, $p = 0.001$). The ANOVA test also showed a significant effect of the interaction between temperature × water potential on germination percentage ($F = 3.45$, $p = 0.001$) (Fig. 2b). All water potentials showed no significant differences in germination percentage at 24 °C and 28 °C, but in the −0.6, −0.3, and −0.15 MPa treatments, germinability was lower at 32 °C compared with 24 °C and 28 °C. Higher germination (94% to 81%) was observed at 24 °C and 28 °C with 0 to −0.15 MPa, compared with the other combined treatments. The lowest germination (23%) was recorded at −0.6 MPa and 32 °C.

The germination of *Populus luziarum* and *P. primaveralepensis* seeds in the different treatments followed a sigmoid curve, with the highest percentage recorded at 12 hours (Fig. 3). For both species, the lowest germination was obtained at −0.6 MPa and 32 °C, and the highest at 0 MPa across the three temperature treatments.

Temperature and water potential had different effects on T_{min} in both species. *Populus luziarum* was affected by water potential ($\chi^2 = 56.66$, $p = 0.001$) but not by temperature ($\chi^2 = 0.2665$, $p = 0.9$). *P. luziarum* began germination at the seventh hour under 0, −0.07, −0.15, and −0.3 MPa, while at −0.6 MPa, germination occurred at the ninth hour regardless of temperature (Fig. 3a–c). The T_{min} of *Populus primaveralepensis* was affected by temperature ($\chi^2 = 26.106$, $p = 0.001$) and water potential ($\chi^2 = 19.217$, $p = 0.001$). Germination began within the first two hours at 0 MPa at both 24 °C and 32 °C (Fig. 3d, f) and at the third hour at 28 °C (Fig. 3e). It was observed that T_{min} increased as water potential decreased; however, this trend was not observed with increasing temperature in either species (Table 1).

The mean germination rate (MGR) of *Populus luziarum* showed significant differences by temperature ($F = 11.46$, $p = 0.001$), water potential ($F = 11.21$, $p = 0.001$), and the temperature × water potential interaction ($F = 4.69$, $p = 0.001$). The highest MGR was recorded at 28 °C. Significant differences were observed at 24 °C and 32 °C. A general trend of decreasing MGR with decreasing water potential was found, except at 32 °C. The combination of 0 MPa and 28 °C resulted in the highest average MGR (Fig. 4a). The slowest MGR was 0.0738 $hours^{-1}$, recorded at −0.6 MPa and 24 °C. At 28 °C and 0 MPa, the MGR was 1.3 times faster (0.0959 ± 0.001 $hours^{-1}$).

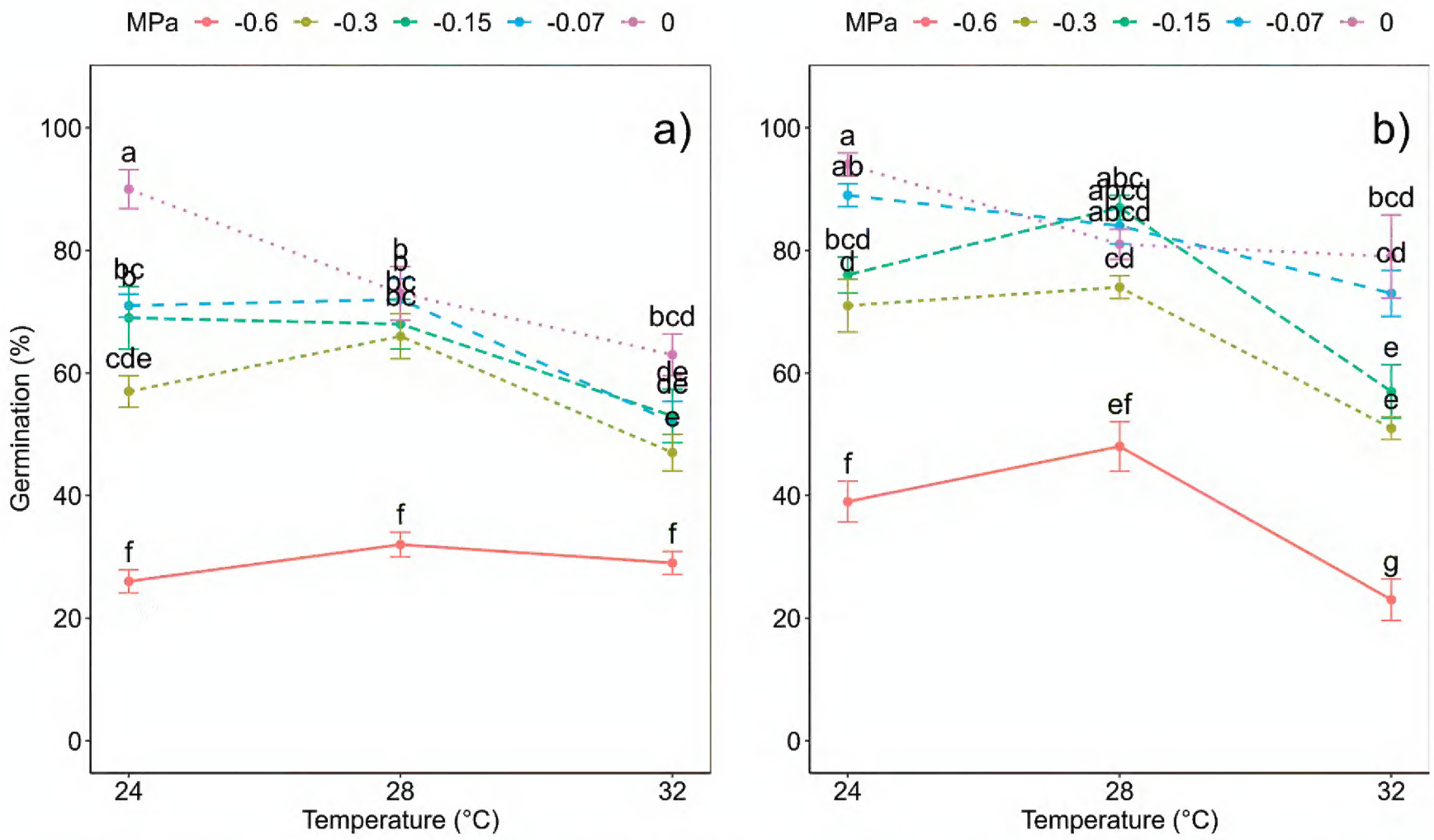

Figure 2. Effect of temperatures (24, 28, and 32 °C), water potentials (0, −0.07, −0.15, −0.3, and −0.6 MPa), and interaction of factors on the germination percentages of seeds of (**a**) *Populus luziarum* and (**b**) *Populus primaveralepensis*. Different letters indicate statistical differences between means, determined by Student–Newman–Keuls multiple comparisons (α = 0.05).

Table 1. Effect of temperature and water potential on the minimum time (T_{min}) required for seeds to begin germinating (hours) in *Populus luziarum* and *P. primaveralepensis*.

Factor	Species	
	Populus luziarum	***Populus primaveralepensis***
Temperature (°C)		
24	7.32 a	2.20 a
28	7.19 a	3.04 b
32	7.32 a	1.64 a
Water potential (MPa)		
0	8.0 a	1.44 a
−0.07	8.0 a	1.44 a
−0.15	8.0 a	2.20 ab
−0.3	8.12 a	2.32 ab
−0.6	9.28 b	3.08 b

Different letters indicate statistical differences according to Holm's procedure (α = 0.05).

The MGR of *Populus primaveralepensis* also showed significant differences by temperature (F = 31.54, p = 0.001), water potential (F = 8.22, p = 0.001), and the temperature × water potential interaction (F = 2.11, p = 0.01). The MGR response was similar to that of *P. luziarum* in terms of temperature, water potential, and their interaction. The slowest MGR was 0.09 ± 0.003 $hours^{-1}$ at −0.6 MPa and 24 °C, while the fastest MGR was observed at 28 °C and 0 MPa, reaching 0.177 ± 0.009 $hours^{-1}$ nearly twice as fast (Fig. 4b). In general, the MGR was very fast for both species, with a tendency to increase with rising temperature up to 28 °C and higher water availability.

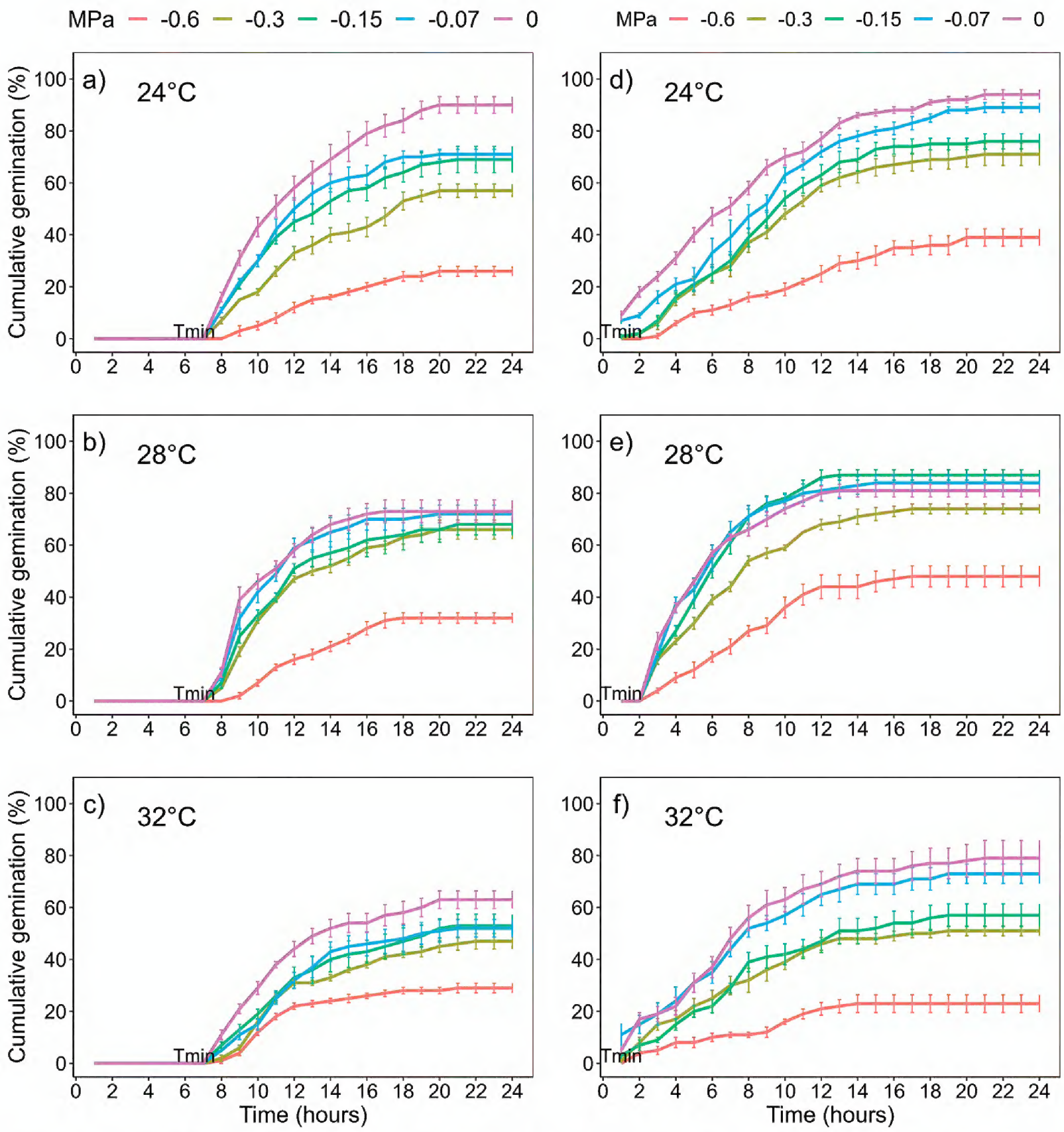

Figure 3. Minimum time and cumulative germination over 24 hours at three temperatures (24, 28, and 32 °C) and five water potentials (0, −0.07, −0.15, −0.3, and −0.6 MPa) for *Populus luziarum* (**a–c**) and *Populus primaveralepensis* (**d–f**), respectively.

Discussion

The hypothesis put forward in this study was confirmed, as the germination of both *Populus* species decreased and slowed under rising temperatures and reduced water potential. Optimal environmental conditions, such as temperature and humidity, are crucial for successful germination and natural establishment (Castro-Morales et al. 2014; Dürr et al. 2015). Moreover, germination is one of the most critical stages in a plant's life cycle and can influence population dynamics and community structure (Harper 1977; Huang et al. 2016). Rapid seed hydration is essential to initiate germination, and a permeable seed coat that facilitates water absorption may accelerate this process. Previous studies have shown that expedited imbibition enabled by a permeable coat favors rapid germination (Drezner and Fall 2002; Karrenberg et al. 2002; Li et al. 2006; Liu et al. 2011). Salicaceae, including *Populus*, possess these characteristics. In addition, *Populus* species are capable of germinating across a

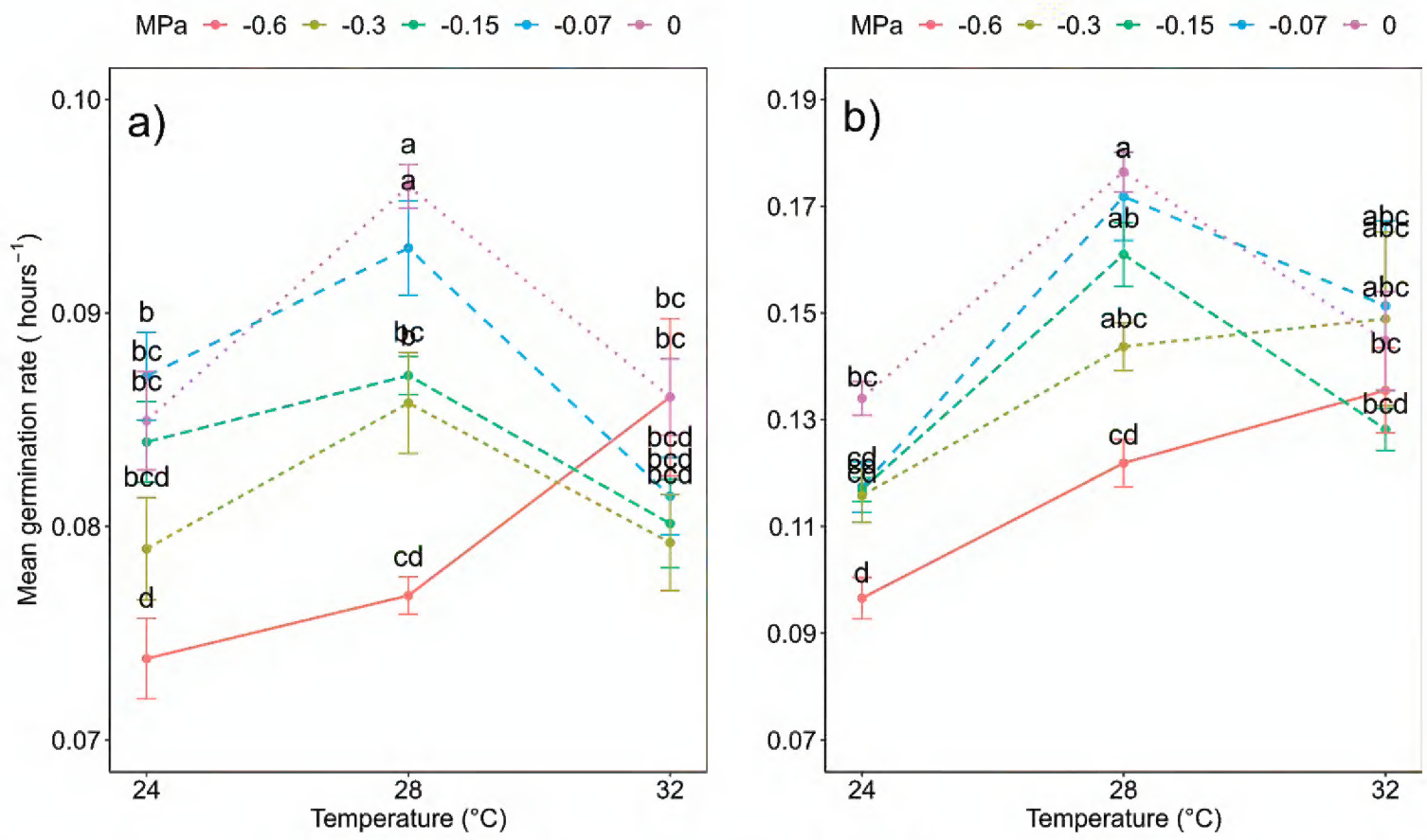

Figure 4. Mean germination rate (hours^{-1}) of (**a**) *Populus luziarum* and (**b**) *Populus primaveralepensis*, evaluated by temperature (24, 28, and 32 °C), water potential (0, −0.07, −0.15, −0.3, and −0.6 MPa), and their interaction. Different letters indicate statistical differences between means, determined by Student–Newman–Keuls multiple comparisons (α = 0.05).

wide temperature range (10–40 °C) (Densmore and Zasada 1983; Siegel and Brock 1990; Van Splunder et al. 1995; Li et al. 2006). However, when high temperatures are coupled with low water potential, both germination and seedling recruitment are at risk. Under these conditions, soil water availability becomes a limiting factor, further decreasing germination.

There was a similar pattern in which the T_{min} occurred very quickly in the *Populus* spp. distributed in the Holarctic region, as *Populus grandidentata* took less than seven hours (Faust 1936), *P. deltoides* took about eight hours (Noble 1979), and *P. euphratica* took less than four hours (Liu et al. 2011). For *P. luziarum* and *P. primaveralepensis*, minimum germination time (T_{min}) was less than eight hours and one hour, respectively. However, decreasing the water potential delayed the T_{min} in a similar way as with *P. fremontii*, which increased the T_{min} when the water potential was decreased (−0.4 MPa) (Siegel and Brock 1990).

This behavior is because *Populus* seeds are permeable, non-dormant, lacking endosperm, and filled by the embryo; some species have recalcitrant seeds and no dry-tolerant characteristics (Parsons et al. 2014; Kim 2018). This means the fast germination between *P. luziarum* and *P. primaveralepensis* may be caused by the lack of reserve tissue. Furthermore, these characteristics suggest that the time in which seeds are viable is brief, and at least for these two species, germination decreases with increasing storage time (Parsons et al. 2014; Parsons 2012; Karrenberg et al. 2002). By contrast, permeable and dormant seeds with a small embryo embedded in an endosperm need a long soaking time to allow the embryo to grow and may take a few days to germinate (Vandelook et al. 2012; Baskin and Baskin 2014; Parsons et al. 2014). Moreover, the fast germination in both species in this study would be decisive to escape from granivore predation, giving them a chance to be established in comparison with slow-germinating seeds (Chen and Xie 2007; Yan et al. 2011; Parsons et al. 2014; Jacobo-Pereira et al. 2022). Very fast germination, in this case, could promote rapid establishment during the rainy season, which is three months before winter begins.

The results of this study indicate that germination of *Populus luziarum* and *P. primaveralepensis* decreases due to the interaction between rising temperatures (> 4 °C) and decreased water potential (−0.15, −0.3, and −0.6 MPa), conditions expected under climate change scenarios in their natural range (IPCC 2014; Ruiz-Corral et al. 2016). These findings highlight the vulnerability of seed germination to environmental stressors and underscore the need to understand the physiological mechanisms governing this process under changing climatic conditions (Priatama et al. 2022; Baskin and Baskin 2014).

Mainly, the germination percentages of *Populus luziarum* and *P. primaveralepensis* were both less than 50% at −0.6 MPa, which is the point at which the basal water potential was reached. This is defined as the water potential at which the germination percentage is 50%, beyond which germination is inhibited because the water absorbed by the seed cannot activate metabolic processes such as the rehydration of membranes, proteins, and DNA (Daws et al. 2008; Zhang et al. 2020). This result shows an increase in the effect of drought stress on germination, and similarities have also been found in other plant families (Patanè et al. 2013).

Nevertheless, when exposed to a water potential of 0 MPa and a temperature of 24 °C, both species had germination percentages of 90% and 94%, respectively. Our results suggest that the increase in temperature (28 °C and 32 °C) during the month in which the seeds are exposed to their habitat could have a negative effect on reducing the germination percentage or even inhibiting the germination of these species. These findings are consistent with those reported by Li and collaborators (2006) for *Populus euphratica* and *P. pruinosa*, which showed low germination percentages as the water potential decreased, reaching a minimum of 5% at −0.9 MPa (*P. euphratica*) and almost 0% at −0.6 MPa (*P. pruinosa*) at temperatures of 10 °C and 40 °C. However, the interaction between factors in that study was not evaluated. Similar results were registered in riparian species in temperate climates such as *Salix alba*, *S. triandra*, *S. viminalis*, and *Populus nigra*, where the germination percentage decreased by 80–100% as a result of thermal variation from 5% to 25% at water potentials of −0.1 to −0.3 MPa (Van Splunder et al. 1995).

Mexican riparian *Populus luziarum* and *P. primaveralepensis* are sensitive to climate fluctuation, which may occur as a function of local adaptations and their geographic distribution with an affinity for wet zones. If droughts are prolonged and temperatures increase, it will affect *Populus* spp. reproduction, which may cause a decrease in their populations (Condit et al. 1996). In future studies, it is necessary to investigate the development and survival of seedlings from seeds germinated under different conditions of water and heat stress to better understand the responses of these seedlings to environmental factors generated by climate warming.

Conclusion

Optimal temperature and humidity are crucial for the successful germination of *Populus* seeds in the Neotropical region of Mexico. Furthermore, the very fast germination observed in both studied species is decisive for escaping predation and provides a competitive advantage for establishment compared to species with slower germination. For both species, germination percentage decreased with increasing temperatures and decreasing water potential. Our findings show that the germination of *Populus luziarum* and *P. primaveralepensis* seeds may be negatively affected by projected global and regional warming.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Use of AI

No use of AI was reported.

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Author contributions

CJP, FMHM, JF, AERL, and AMU wrote this article. CJP, AMU, and JF conceived and designed the experiments. CJP and AMU conducted the experiments. CJP, AMU, and FMHM performed the statistical analyses. CJP, FMHM, JF, AERL, and AMU critically reviewed the study.

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Data availability

All of the data that support the findings of this study are available in the main text.

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